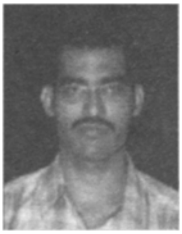
Donald Redfield Griffin

The Discovery of Echolocation

H Raghuram and G Marimuthu



H Raghuram is a graduate student working on prey detection and echolocation in the carnivorous bat *Megaderma lyra*.

G Marimuthu works on the biology and behaviour of bats. His present research deals with pollination biology of fruit bats and prey capture by the Indian false vampire bat.

The puzzle as to how bats navigate without colliding with obstacles and hunt tiny mosquitoes in complete darkness remained unanswered for nearly 140 years after Lazzaro Spallanzani, who proposed at the close of the 18th century that bats possess a 'sixth sense' for orientation. Donald Griffin solved the puzzle in 1938 with the help of world's first ultrasound microphone devised by the American physicist G W Pierce. Griffin called this sixth sense 'echolocation', which enables bats and marine mammals such as whales, dolphins and porpoises to lead active lives under the cover of darkness. In this article we describe the life of Donald Griffin and how he proved the existence of echolocation in bats.

Donald Redfield Griffin was born in Southampton, New York on 3rd August 1915. He received his bachelors, masters and doctoral degrees from Harvard between 1938 and 1942. He was a faculty at Cornell and later Professor of Zoology at Harvard from 1953 to 1965. He was granted tenure at Rockefeller and remained there as an Emeritus Professor of animal behaviour until his retirement in 1986.

Internationally renowned for his work on animal behaviour, animal navigation, acoustic orientation and sensory biophysics, he was one of the first scientists to challenge the dogma that animals are mindless automatons, controlled solely by instinct and reflex. He not only performed innovative and complex experiments in the laboratory, but also pioneered the use of rigorous techniques to study birds and mammals in their natural environment. A major characteristic of his work is the scale of his experimental designs. Griffin's own research has ranged

Keywords
Discovery of echolocation, Donald Griffin, bats, magic well.

from probing the mysteries of bird migration to analyzing the underwater hearing capabilities of fish. However, he is best known for his discovery of echolocation, a phenomenon he named back in 1944. It will be interesting to look back at the history and the experiments conducted by Griffin that led to the discovery of echolocation.

Griffin's own research has ranged from probing the mysteries of bird migration to analyzing the underwater hearing capabilities of fish. However, he is best known for his discovery of echolocation.

A Historical Perspective of Echolocation

Our understanding of how bats use hearing began in the last years of the eighteenth century. The great Italian scientist, Lazzaro Spallanzani (1729-99), noted that blinded bats could fly, avoid obstacles, land on walls and ceiling, and survive in nature as well as bats with sight. Spallanzani wrote about his discovery in a letter to Geneva Natural History Society in 1793 that drew the attention of the Swiss zoologist Charles Jurine. Jurine added one more decisive experiment to the series; if ears of a bat were tightly plugged with wax or other materials, it blundered helplessly into obstacles. In 1794, Spallanzani repeated this experiment and obtained similar results. Both Spallanzani and Jurine concluded that "bats require their sense of hearing in order to find their way". George Cuvier (1769-1832), a French naturalist, openly criticized their experiments in his paper that was published in1800. According to Cuvier, the sense of touch in the body surface or wing membrane would explain the bat's ability to avoid obstacles. At that time, this seemed to be a more plausible explanation and was accepted by zoologists for over a century and virtually no further experiments were conducted until the early 1900's.

In 1908 Hahn, a young American zoologist at Indiana University, repeated the experiments performed by Jurine and Spallanzani. He added the feature of regularly spaced vertical wires to calculate quantitative scores in the form of percent hits and misses under various conditions. Hahn also found that bats were impaired when their ears were plugged and concluded that obstacles were perceived chiefly through sense organs located in the internal ear.

Griffin's Investigation with Bats

As an undergraduate student of biology at Harvard in the 1930s, Griffin studied bat migration and homing through banding. Two hypotheses proposed by Maxim and Hartridge (*Box* 1), made Griffin to think further on experiments with bats. It was obvious that low frequency sounds were not sufficient to gather enough information for bats, so he neglected Maxim's hypothesis and proposed to work on the opposite hypothesis postulated by Hartridge. Griffin visited the physics professor, George Washington Pierce, who helped him with an apparatus to analyze "supersonic sounds". During those days this was the only apparatus in the entire world that could detect and analyze sounds over a broad frequency range extending from the upper limit of human hearing of about 20 kHz (*Table* 1). Pierce actually used this apparatus to study the sounds of insects. The apparatus consisted of a parabolic horn with a Rochelle salt microphone at its focus, vacuum tube amplifiers, and a heterodyne receiver tunable from about 10 to 150 kHz. The apparatus reduced the pitch of sound signals so that they could be heard

Box 1. Low Frequency and High Frequency Hypothesis

After the tragic sinking of the ship *Titanic* in 1912, the American born engineer Sir Hiram Maxim (best known for his invention of the Maxim machine gun) was inspired by the blind bat's flight as a plausibility to prevent future ship collisions. In 1912, he published an article in *Scientific American*, where he reported his conviction that "bats detect obstacles by feeling reflections of the low frequency sounds caused by their wing beats (appx. 15 Hz) and ships could be protected by collisions with ice bergs or other ships by the installation of an apparatus to generate powerful sound and a detection device to receive the returning echoes". Although he never invented the machine, he postulated that bats emit low frequency sounds below the human hearing range..

The British physiologist Hartridge advanced the second hypothesis involving the opposite end of this acoustic spectrum in 1920. Bearing in mind the use of underwater sound signaling during the First World War, Hartridge suggested that bats might use sounds of high frequency and short wavelength (*Table* 1). He too did not perform any experiments, but proposed this hypothesis after watching bats flying skillfully through a darkened room. It was not even clear from Hartridge's paper whether he had in mind high *audible* frequencies of the order of 15 to 20 kHz or frequencies above the range of human ear. But he was the first to emphasize that bats use high frequency sounds.

S. No	Classification	Range	Description	Applications
1	Infra sound	0.1Hz to 25Hz	Short frequency sounds	Infrasound can travel a long distance over 3 km. Therefore, helpful for long distance communication, used by elephants.
2	Audible sound	20Hz to 20kHz	Medium frequency sounds	Human hearing
3	Ultrasound	> 20kHz	High frequency sounds	Ultrasound travels only a short distance. Therefore, helpful for short distance target detection within 10m, used by bats.

Table 1. Physiological classification of sounds.

using a loudspeaker. Pierce enthusiastically invited Griffin to bring some bats (*Figure* 1) to his apparatus. They found that when bats were allowed to fly, their microphone picked up high frequency sounds only occasionally. Their results formed the basis for a paper in the *Journal of Mammalogy* in 1938, which was absurdly cautious and stated that these newly discovered high frequency sounds may have nothing to do with orientation in the dark. Griffin was tempted to work more on bat banding and to study harder for his final exams. Yet these new inaudible sounds were too intriguing to ignore.

So, Griffin planned to design some experiments with a fellow student, Robert Galambos, who was an expert in auditory physiology. The first step Griffin suggested was to test the cochlear

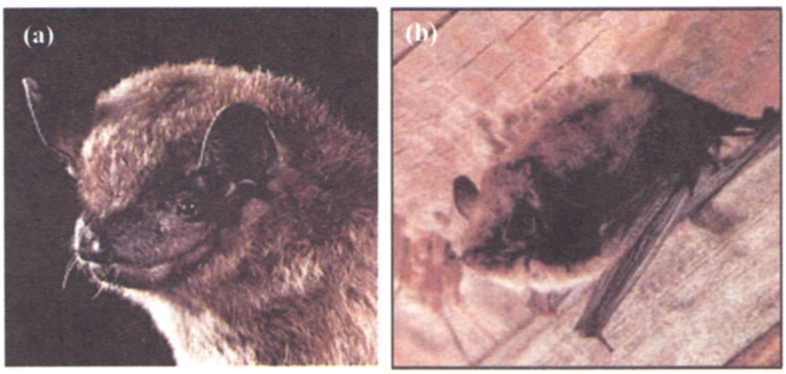


Figure 1. Bat species first used to study echolocation (a) Eptesicus fuscus (big brown bat), (b) Myotis lucifugus (little brown bat). (Photo credit: Merlin Tuttle, BCI)

Pierce and Griffin confirmed that bats increase the ultrasound pulse rate, whenever they faced a difficult problem such as dodging small obstacles.

microphonics of bats. For that, an apparatus was necessary to generate high frequency sounds and to elucidate the cochlear microphonic potentials from bats. The only way was to borrow the apparatus assembled by Hallowell Davis at the Harvard Medical School. Pierce graciously agreed to lend this only available apparatus that could generate controlled sounds above the frequency range of human hearing. Unfortunately, Griffin and Galambos did not realize that the ordinary-looking power outlets in the medical school supplied DC and not AC power. Therefore their first experiment yielded a puff of smoke and a serious diplomatic problem. With the repaired apparatus they discovered that bat cochleae generate microphonics up to about 100 kHz. They also found that if the Pierce's microphone was held directly in front of a flying bat, high-frequency sounds were easily and consistently detectable. Pierce and Griffin had not realized earlier that this apparatus could detect bats only when they flew toward the microphone because of the directionality of both the parabolic horn and the beams emitted by bats. Pierce and Griffin confirmed that bats increase the ultrasound pulse rate (*Figures* 2-4, *Box* 2), whenever they faced a difficult problem such as dodging small obstacles. In the second step, they repeated the quantitative experiments done by Hahn in 1908 to measure obstacle avoidance ability of bats under various conditions. With extensive alterations, they repeated the experiments of Jurine and Hahn and reconfirmed that covering the ears of bats resulted in total disorientation. These surprising results were published in a series of papers in 1940.

In 1943, Sven Dijkgraaf of Holland independently discovered bat echolocation without the benefit of any electronic apparatus. By listening carefully as bats flew about in quiet surroundings he was able to hear the faint audible component which accompanies the ultrasonic orientation sounds. He named this audible sound *ticklaut*. This and what Griffin and Galambos called the audible click accompanying the physically much more intense ultrasonic signals were clearly one and the same. Griffin straightened these matters through cordial correspondence by sending

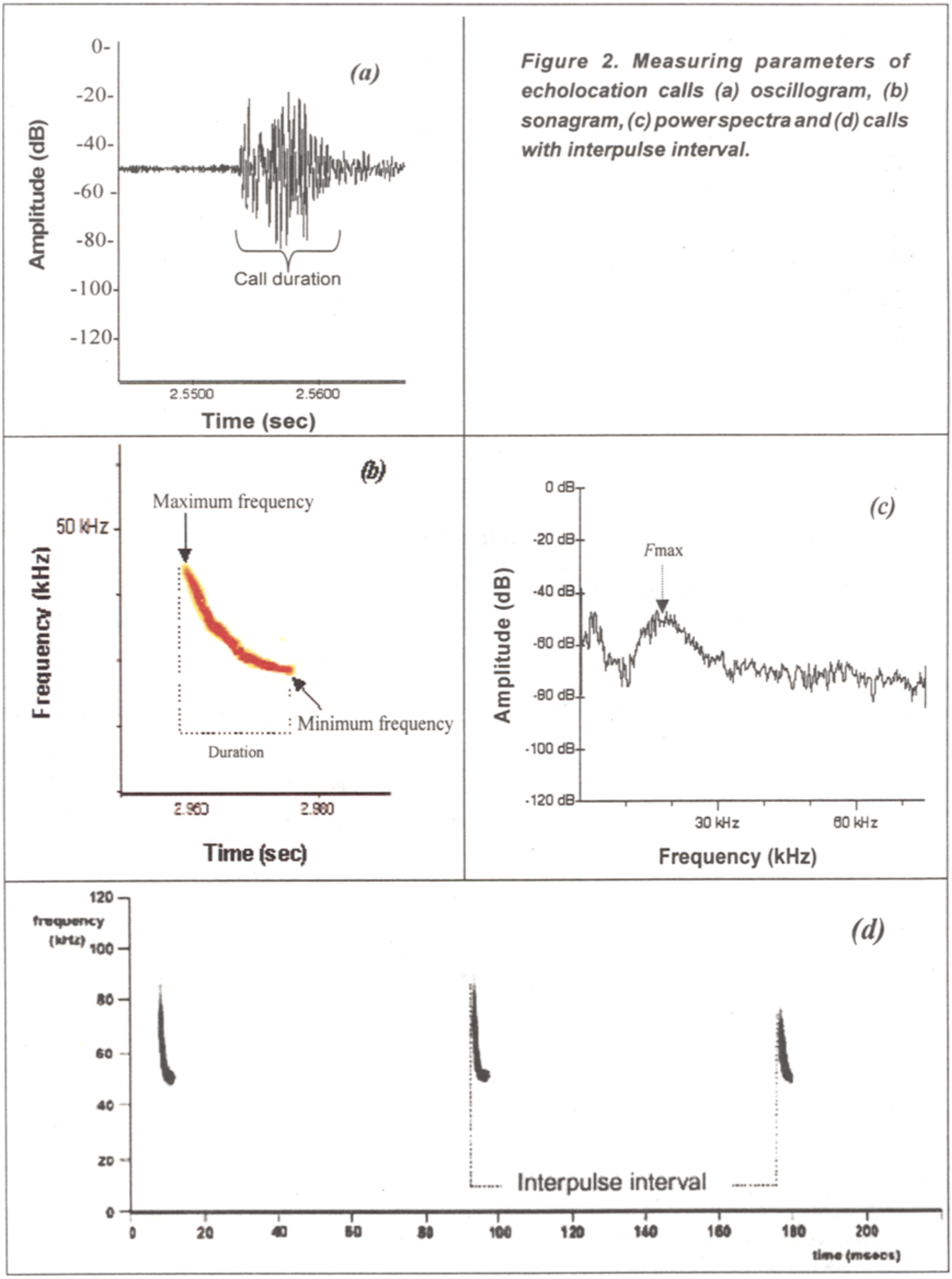


Figure 2. Measuring parameters of echolocation calls (a) oscillogram, (b) sonagram, (c) power spectra and (d) calls with interpulse interval.

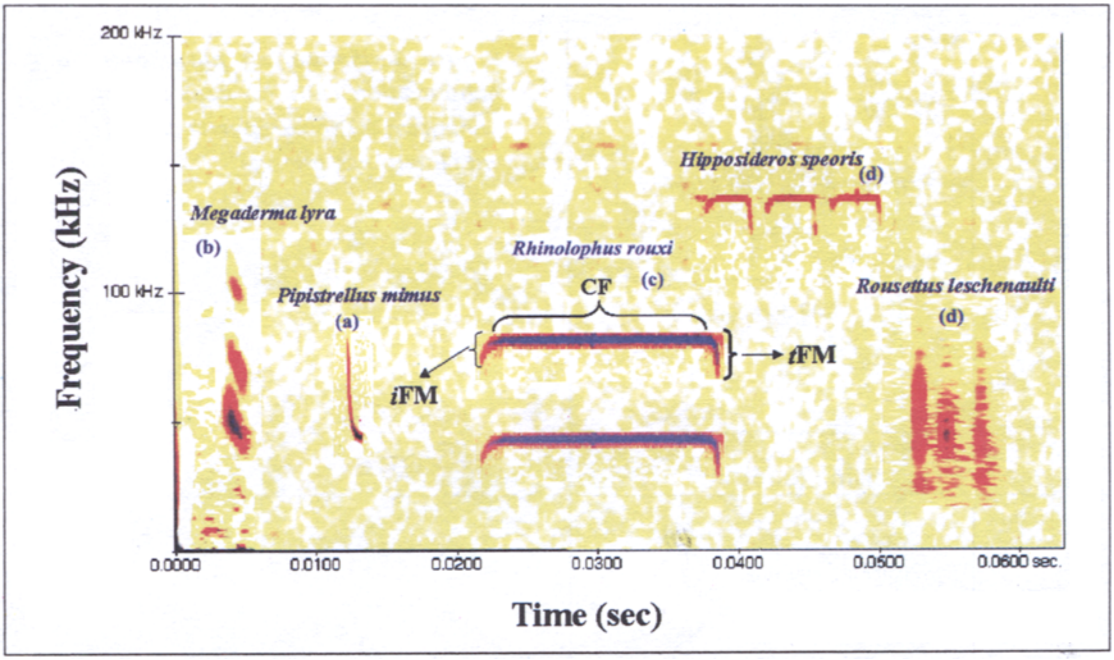


Figure 3. Sonagram representation of echolocation calls of different south Indian bat species. (a) Frequency modulated (FM) type calls without harmonics, (b) FM type calls with harmonics, (c) FM-CF-FM type calls characterized by an initial frequency modulated component (iFM) followed by a long constant frequency component (CF) and ending with a terminal frequency modulated call (tFM), (d) CF-FM type calls, note the constant frequency calls ending with FM tails (e) tongue clicks similar to FM but no structure.

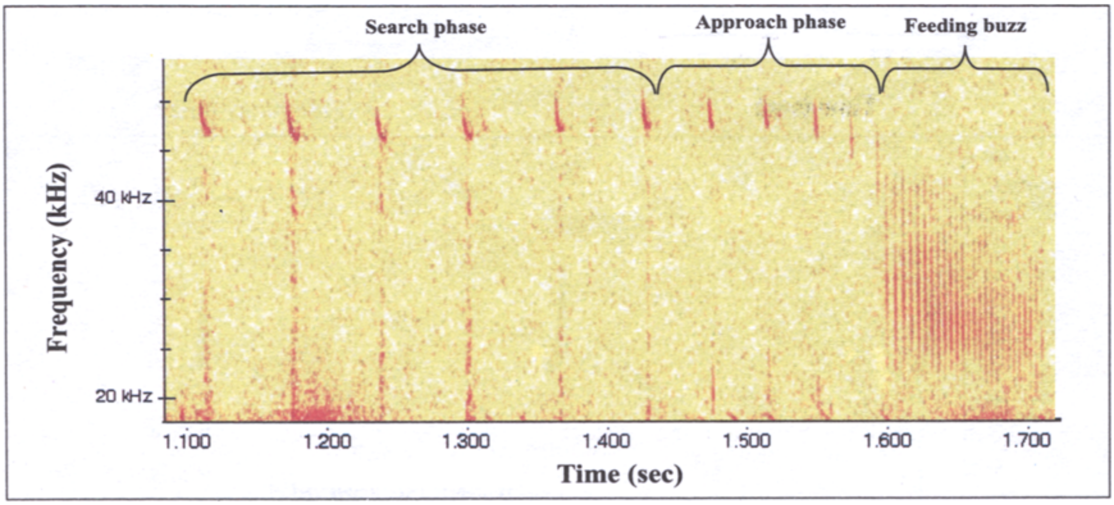


Figure 4. Echolocation call sequence of Pipistrellus mimus during prey capture recorded near a street lamp during winter. Note the changes in interpulse interval during search, approach and capturing phase (feeding buzz or terminal buzz).

Box 2. Basics of Echolocation in Bats

Echolocation, the sonar 'sight' of bats, is analogous to the sonar used by the military. Because it is produced by living organisms rather than by machines, it is often called 'biosonar'. A simple definition is that it is the analysis by an animal of the echoes of its own emitted sound waves, by which it can build a sound picture of its immediate environment.

While bats of sub-order Microchiroptera and marine mammals of the order Cetacea (whales and dolphins) are the two groups in which echolocation is well developed and well studied, there are isolated cases in cave-dwelling birds (swiftlets), oil birds and suggestive evidence that it may occur in a rudimentary form in some terrestrial shrews and rodents. It is also sometimes attributed to seals, rats and humans, but the evidence for this is not conclusive.

All microchiropteran bats produce èholocation calls using vocal cords in their voice boxes, or larynges. In contrast, the only echolocating fruit bat *Rousettus* species emit sounds by clicking their tongues. Different species broadcast calls in different ways, some emitting calls from the mouth and others through their nostrils. Oral emitters fly with their mouths open, and nasal emitters fly with their mouth closed. Remarkably, both kinds of bats can chew food and vocalize at the same time.

Although the calls of most bats are not audible to the human ear, the loudness of bat echolocation calls can still be measured. This is expressed in decibels (dB), and for comparison is usually measured at a fixed distance from a bat's mouth (at 10 centimeters or about four inches). Intense echolocation calls measure 110 dB or more (equivalents in strength to a smoke detector alarm). Faint echolocation calls measure as little as 60 dB (the intensity level of normal human conversation). The Indian pygmy bat *Pipistrellus mimus* is an example of high intensity, or 'shouting'echolocators, while the Indian false vampire bat *Megaderma lyra* is an example of low intensity, or 'whispering' bats. The echolocation calls of bats differ with respect to their environment where they forage. Bats that feed in open spaces produce the most intense calls. In contrast, those that forage in cluttered areas, such as deep in the forest, usually produce low intensity calls.

Although the intensity of bat sound is so high, we cannot hear it because it is of high frequency. Frequency is measured in kilohertz (kHz), where one hertz is one cycle per second. The frequencies used in echolocation by bats fall usually between 25 and 100 kHz, although some species emit ultrasonics as high as 200 kHz.

Bats emit echolocation sounds in pulses. These pulses are usually frequency modulated (FM), constant frequency (CF) or combinations of both. The calls may be broadband or narrowband. Thus bandwidth refers to the range of frequency of the calls emitted by bats. *Megaderma lyra* emits broadband sounds from 20 to 120 kHz, while *Hipposideros speoris* is a narrowband echolocator emitting constant frequency sounds of 135 kHz (*Figure* 3d). Hence the terms broadband for FM sounds and narrowband for most CF sounds.

Box 2 continued...

Box 2 continued...

FM pulse is characterized by a short, steep sweep down the frequencies, from about 60 to 30 kHz over 5 ms in many vespertilionids like *Pipistrellus mimus* (*Figure* 3a). FM may be characterized by the presence of harmonics (i.e. integral multiples of the fundamental frequency, e.g. if 20 kHz is the fundamental then the pulse is characterized by increasing order of 40, 80, 100 kHz and so on). *Megaderma lyra* produces a broadband FM call with 4 to 6 harmonics (*Figure* 3b). *Figure* 3b represents calls characterized by three harmonics. In contrast, *Rousettus leschenaulti* produces a typical pattern of sounds referred to as clicks. They have very short duration of 1ms and are similar to FM but do not have specific structure like FM or CF calls type (*Figure* 3e).

Constant-frequency signals have a long duration of 10-100 ms with a brief FM sweep at one or both ends. CF pulses show a lot of interspecific variations and are more accurately referred to as CF/FM or even FM/CF/FM pulses. *Hipposideros speoris* produces CF/FM calls whereas *Rhinolophus rouxi* emits a characteristic FM/CF/FM calls (*Figure* 3c).

The sequence of events of sound production leading to a successful capture is shown in *Figure* 4. During the search phase, as a bat hunts for its prey, the number of pulses is low with large interpulse interval (*Figure 2d*). When it detects prey, the bat enters the approach phase: as it moves closer, there is a shorter distance between bat and prey and therefore less time between pulse and echo. So the pulses have to get shorter to avoid overlap. The bat also updates its rate of emission as it gets progressively faster. In the terminal phase, pulses may be only a fraction of millisecond long and results in a feeding buzz. The same occurs when they fly close to walls or obstacles.

Echolocation calls emitted by bats can be recorded using a bat detector, where the sound is transferred to a Portable Ultrasound Processor (this digitally stores three seconds of 'real' time, and slows it down by a factor of ten) and stored in a Sony Professional Walkman. The recorded sounds can be conveyed to a computer and with the aid of BatSound Software, we can analyze various call parameters in graphical representations as sonagram, oscillogram and power spectra (*Figures* 2 a-c). The oscillogram gives the onset and offset of a call. Sonagram provides the duration, maximum and minimum frequency of the calls. From power spectra we can measure the maximum frequency (*fmax*) of the call which bats emphasize at different situations (*Figure* 2 c). The most important parameters are the duration (*Figures* 2 a, b) and interpulse intervals of the calls (*Figure* 2 d).

a live bat *Myotis lucifugus* to Dijkgraaf to compare sound emissions of his bat with that of the very closely related European species he had studied.

After the Second World War, Griffin analyzed the sounds of bats more accurately than had been possible with Pierce's original apparatus. He found that bats could detect tiny objects such as wires 0.2mm in diameter. Meanwhile, the notion of sensing objects by means of reflected sound signals became more widely accepted as sonar and radar came into public awareness once the veil of wartime military secrecy was removed.

The notion of sensing objects by means of reflected sound signals became more widely accepted as sonar and radar came into public awareness once the veil of wartime military secrecy was removed.

Michael Supa, a blind student, along with fellow student Milton Cotzin, investigated the echolocation ability of the visually impaired, under the guidance of K M Dallanbach of Cornell. In 1944, they showed that many who are blind, can detect obstacles by making sounds and hearing reflections or change in these sounds. This led Griffin to suggest the term 'echolocation' for the process by which animals locate objects that they cannot see or touch by emitting signals and analyzing the returning echoes. In 1958, he summarized his findings in a book '*Listening in the dark – acoustic orientation of bats and men*'. Griffin turned to simple observations on wild bats hunting insects. He wondered vaguely whether echolocation played a role in hunting, even though the prevailing view was that bats either saw their prey, or listened for the sounds of wing beats and located insects by passive hearing. When Griffin set up an apparatus beside a small pond where bats were actively hunting, it was a dramatic to see trains of ultrasonic pulses on the oscilloscope screen. When bats flew toward obstacles in the laboratory, they roughly doubled the repetition rate of their orientation sounds. But when bats pursued flying insects the repetition rate increased tenfold or more. Griffin called this increasing pulse rate (e.g. 200 per second) as *feeding buzz* that occurred during the terminal phase of capturing an insect (*Figure* 3). His observations strongly suggested that bat sonar was helpful to guide the rapid and complex maneuvers during insect pursuit and capture.

In later experiments, Frederic Webster and Griffin showed that bats could catch fruit flies just as rapidly in darkness. For this experiment, fruit flies had to be brushed into the air at frequent intervals to provide good hunting for their bats. Griffin thought up a brilliant scheme; he made a '*Drosophila* fountain' of freshly frozen fruit flies propelling and returning back to the same place. Griffin was sure that the bats would find this excellent

From 1938 to 2001, Griffin published more than hundred papers in reputed journals such as *Nature, Proceedings of the National Academy of Sciences USA,* and *Animal Behaviour.* Many of them are citation classics that are quoted even today.

hunting since he already knew that they ate freshly killed insects. But the bats fooled him once again by totally ignoring the dead fruit flies. At that time, this was just one more unexplained frustration for him. Eventually, Webster was successful in inducing bats to catch mealworms tossed up to them from the floor and they began to study whether bats could discriminate between targets of roughly similar size. They tossed two different sized disks among mealworms and found that bats were more proficient to catch mealworms. They concluded that bats were able to distinguish between the nature of echoes from the disks and mealworms. Thus Griffin reaffirmed that echolocation was much more than a mere collision warning system.

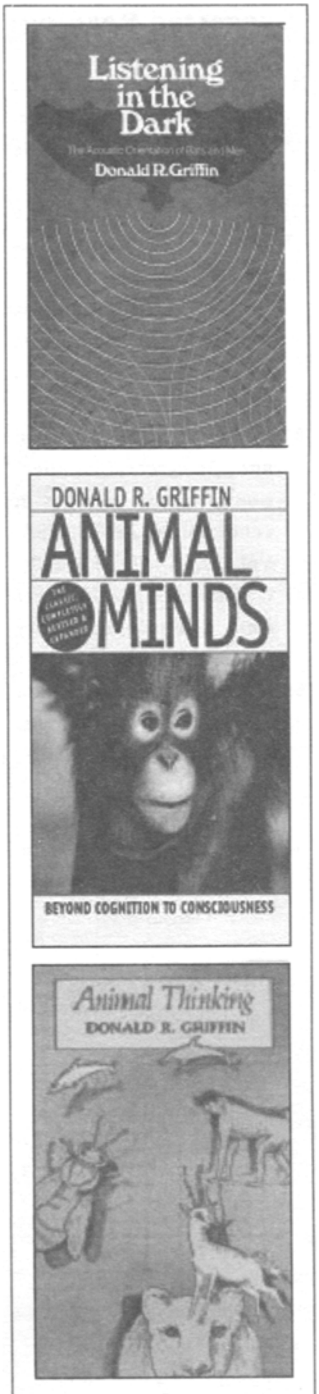
In 1971, Griffin reported the importance of atmospheric attenuation of sound in the echolocation of bats. He showed that the range of echolocation was quite restricted. Basically, sound is attenuated in air by two processes: (1) Geometric attenuation – the sound pressure of the emitted signal, which can be described as a circular wave, decreases as the square of the distance from the transmitter and (2) Absorption – sound absorption in air is greatest for high frequencies and also increases with humidity and temperature. Therefore, low frequencies have a longer range. In echolocation, the path traveled by sound is doubled because it must travel from the bat to the reflecting object and then back. Because of these physical constraints, echolocation can operate only over a limited range, usually within 10m. From 1938 to 2001, Griffin published more than hundred papers in reputed journals such as *Nature, Proceedings of the National Academy of Sciences USA*, and *Animal Behaviour*. Many of them are citation classics that are quoted even today.

In describing the wealth of new knowledge gained in his work with honey bees, Karl von Frisch called honey bee behaviour a 'magic well' because the more he learned about their orientation and communication, the more surprising and significant discoveries came to light. Likewise Griffin called the echolocation behaviour of bats another magic well. Amazing discoveries from several bat species came to light at the end of the 20th century.

Box 3. Books written by Donald Griffin

Griffin has written 8 books and contributed to about 14 books. We consider here a few books that are 'citation classics'. His first book *Listening in the Dark – The Acoustic Orientation of Bats and Men* is written in a simple, lucid and logical style and is ideal reading for one who starts research in bats especially on echolocation. This book won the Daniel Giraud Elliot medal of National Academy of Sciences, USA. With the perspective of 20 years of subsequent work in the field, it will be astonishing to anyone re-reading this classic to realize how fully Griffin already understood the phenomenon of echolocation, how many critical discoveries he had already made, and how profound were his insights.

In 1976, he wrote the book *The Question of Animal Awareness* where he suggested that animals could have conscious minds like those of humans and capable of thought and awareness. The idea has been proposed by other scientists, including Charles Darwin who wrote a book on this issue, but was considered very controversial. Critics said animals could be programmed like computers to perform behaviours without consciousness. Despite the skeptics, Griffin continued to explore the topic, publishing *Animal Thinking* in 1984. In 1992, in another book *Animal Minds: Beyond Cognition to Consciousness*, with significant examples of versatile behaviour, he explained conscious thinking in animals. Some of them are: scrub jays that exhibit all the objective attributes of episodic memory, observations that suggested monkeys sometimes know what they know, creative tool-making in crows, and recent interpretation of goal-directed behaviour of rats as requiring simple non-reflexive consciousness.



Citation classics of Donald Griffin.

Recent elaborations and technical advancements have helped to answer the problems that frustrated Griffin like his failure with the *Drosophila* fountain.

Echolocating animals can determine not only the location of an echo source, but they can also perceive its size, form, and surface texture. It would therefore be more accurate to speak of 'echo perception' or 'echo imaging'. In 2003, Otto von Helversen and Dagmar von Helversen proved that the glossophagine (nectar feeding) bats find new nectar sources not only by the special odour of chiropterophilous (bat) flowers but also by recognizing the specific shape and texture of the flowers by echolocation. These bats discriminate buds, virgin and exploded flowers using echolocation. Again in 2004, researchers from Germany showed that bats could perceive not only the position of an object in darkness but also recognize its 3D structure. This is solely due to the nature of echoes from the objects. The echo from a conifer tree is different from a broad-leaf tree. Thus echolocation not only helps insect eating bats to capture mobile prey but also helps the plant visiting bats to find their stationary food sources like pollen and nectar.

Finally, can ultrasound help the blind to navigate? Dean Waters from UK has designed a bat-inspired sonar walking stick that could help the visually impaired sense their surroundings. This lightweight device emits sound too high-pitched for the human ear to detect. It also picks up the reflections of these waves to map obstacles up to three metres away in three dimensions. Buttons on the cane's handle vibrate gently to warn a user to dodge low ceilings and sidestep objects blocking their path. These canes cost around £400 (approx. Rs.33, 000/-) each. Thus the study of echolocation has enabled us find new ways to help the visually impaired.

Griffin died on 7th November 2003 at his home in Lexington, Massachusetts. He was 88. His wife, Jocelyn Crane died in 1998. He is survived by two daughters and a son. Brock Fenton, a well-known bat-researcher in Canada said "Don took us to the magic well of echolocation. It is his well, but he always shared it, and he will ever be with those who go there. The well is still pumping".

Suggested Reading

[1] D R Griffin, *Listening in the Dark – the Acoustic Orientation of Bats and Men*, Yale University Press, 1958.

[2] D v Helversen and O v Helversen, Object recognition by echolocation: a nectar-feeding bat exploiting the flowers of a rain forest vine, *J. Comp. Physiol.*, Vol. 189, pp.327-336, 2003.

[3] J E Grunwald, S Schornich and L Wiegrebe, Classification of natural textures in echolocation, *PNAS*, USA, Vol. 101, pp.5670-5674, 2004.

[4] G Neuweiler, *The Biology of Bats*, Oxford University Press, 2000.

[5] G Marimuthu, Echolocation – the strange ways of bats, *Resonance*, Vol. 3, No.5, pp.40-48, 1998.

Address for Correspondence
H Raghuram and
G Marimuthu
Department of Animal
Behaviour and Physiology
School of Biological Sciences
Madurai Kamaraj University
Madurai 625 021, India.
Email:gmari@sancharnet.in
hraghuram@rediffmail.com